

# Wood specific gravity and anatomy of branches and roots in 113 Amazonian rainforest tree species across environmental gradients

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## Summary

- Wood specific gravity (WSG) is a strong predictor of tree performance across environmental gradients. Yet it remains unclear how anatomical elements linked to different wood functions contribute to variation in WSG in branches and roots across tropical forests.
- We examined WSG and wood anatomy in white sand, clay terra firme and seasonally flooded forests in French Guiana, spanning broad environmental gradients found throughout Amazonia. We measured 15 traits relating to branches and small woody roots in 113 species representing the 15 most abundant species in each habitat and representative species from seven monophyletic lineages occurring in all habitats.
- Fiber traits appear to be major determinants of WSG, independent of vessel traits, in branches and roots. Fiber traits and branch and root WSG increased from seasonally flooded species to clay terra firme species and lastly to white sand species. Branch and root wood traits were strongly phylogenetically constrained. Lineages differed in wood design, but exhibited similar variation in wood structure across habitats.
- We conclude that tropical trees can invest differently in support and transport to respond to environmental conditions. Wind disturbance and drought stress represent significant filters driving tree distribution of Amazonian forests; hence we suggest that biophysical explanations should receive more attention.

## Introduction

Wood specific gravity has emerged as central to the ecology of woody plant species as it relates to growth, mechanical strength, efficiency and safety of hydraulic transport, water storage, survival and resistance to herbivory (Jacobsen *et al.*, 2008; Chave *et al.*, 2009; Zanne *et al.*, 2010). Indeed, wood specific gravity reflects plant allocation to support and conduction, which in turn influences the performance and life history strategies of woody plant species (Muller-Landau, 2004; Poorter *et al.*, 2010). Wood specific gravity is a complex trait encompassing properties of various wood elements: vessels as the main sap-conducting cells in angiosperms, fibers as the main support structures, and parenchyma which serves for both storage and transport of resources between xylem and phloem. The tradeoffs involved have led to two non-mutually exclusive hypotheses: (1) wood specific gravity should decrease with increasing vessel fraction, vessel area and vessel density affecting the amount of lumen space in wood (Preston *et al.*, 2006); and (2) wood specific gravity should increase with increasing fiber fraction, because fiber has the thickest cell walls and hence contributes most to the wood matrix (Poorter *et al.*, 2010).

A growing number of studies have tested these two hypotheses (Ackerly, 2004; Preston *et al.*, 2006; Jacobsen *et al.*, 2007a; Zanne *et al.*, 2010; Martinez-Cabrera *et al.*, 2011; Gleason *et al.*, 2012), but few studies have so far integrated all wood anatomical elements to explore their relative contribution to wood specific gravity (Jacobsen *et al.*, 2007a; Pratt *et al.*, 2007; Martinez-Cabrera *et al.*, 2009; Poorter *et al.*, 2010; Lens *et al.*, 2011). Additionally, few studies have investigated the relationship between wood specific gravity and wood anatomy in the hyper-diverse tropical forests and these studies have been limited to a relatively small number of species (Baltzer *et al.*, 2009; Zhu & Cao, 2009; Poorter *et al.*, 2010; McCulloh *et al.*, 2011; Fan *et al.*, 2012; Worbes *et al.*, 2013). Still lacking is an understanding of how wood specific gravity relates to the relative allocation to the different anatomical tissues, especially in tropical tree species.

Furthermore, the study of wood structure in woody plant species is often restricted to main stems and branches (e.g. Jacobsen *et al.*, 2007a; Martinez-Cabrera *et al.*, 2009; Poorter *et al.*, 2010), mostly because of their obvious role in sap transport and mechanical support, but also because of their accessibility. However, wood specific gravity as a functional trait is involved in all woody

tissues, from the roots to the canopy, so it appears crucial to study wood structure in both aboveground and belowground wood systems to better understand wood structure patterns at the whole-plant level (Fortunel *et al.*, 2012). The hydraulic continuity between roots and stems suggests a tight relationship among anatomical traits related to vessels, as defined in the pipe model theory (Shinozaki *et al.*, 1964; Tyree & Ewers, 1991; Blonder *et al.*, 2011). However, the increase in flow resistance and the simultaneous decrease in water potential with path length have led some authors to suggest that vessels should taper along the flow path from roots to stems (West *et al.*, 1999; McCulloh *et al.*, 2003). In addition, the differences in mechanical constraints and storage capacity can lead to independent variations of anatomical traits pertaining to fibers and parenchyma. To our knowledge, roots have been included in only two anatomical studies, which have been limited to a relatively small number of species (nine species in Pratt *et al.*, 2007; five species in Schuldt *et al.*, 2013). Yet these two studies reported equivocal correlation patterns between stem and root wood anatomy.

Several studies have shown that wood specific gravity varies across environmental gradients, with high wood specific gravity observed in plant species growing in dry or nutrient-poor soils (Preston *et al.*, 2006; Martinez-Cabrera *et al.*, 2009; Gleason *et al.*, 2012). Denser wood generally correlates with lower sapwood conductivity, lower wood water storage and thinner bark, but greater resistance to xylem cavitation (Bucci *et al.*, 2004; Santiago *et al.*, 2004; Baraloto *et al.*, 2010b). Denser wood also requires greater construction costs (Enquist *et al.*, 1999), but confers greater resistance to mechanical damage and pathogen attack, leading to slower growth and lower mortality rates (Falster, 2006; Poorter *et al.*, 2008; Cornwell *et al.*, 2009). However, a high wood specific gravity can be achieved with different combinations of wood elements, and so far it remains unclear how wood anatomical traits contribute to woody plant strategies across environmental gradients. To bridge the gap between traits, plant performance and life history strategy, it is thus essential to look at variations in both wood specific gravity and anatomy across environmental gradients.

In addition to the examination of ecological trends in wood structure, several studies have also looked into the evolutionary trends in anatomical traits (e.g. Preston *et al.*, 2006; Zanne *et al.*, 2010; Martinez-Cabrera *et al.*, 2011; Gleason *et al.*, 2012; Poorter *et al.*, 2012). Wood specific gravity appears to be phylogenetically conserved at broad and narrow phylogenetic scales (Cavender-Bares *et al.*, 2004; Chave *et al.*, 2006; Swenson & Enquist, 2007). However, the anatomical design may differ considerably across plant lineages and it remains unclear whether evolutionary changes in wood specific gravity relate to congruent evolutionary changes in wood anatomical traits. The high turnover of plant species among contrasting forest habitats (Baraloto *et al.*, 2007; Fine *et al.*, 2010), associated with changes in plant community functional composition (ter Steege *et al.*, 2006; Kraft *et al.*, 2008), may influence wood trait correlations. In this respect, a broad range of species functional strategies and evolutionary histories is crucial to allow a general test of hypotheses of wood trait coordination.

In the present study, we investigated patterns of wood specific gravity and anatomy of branches and small woody roots by measuring 15 traits pertaining to support, conduction and storage functions on a total of 147 individuals representing 113 species across steep environmental gradients in French Guiana. We focused on the three most common habitats in lowland South American rainforests: seasonally flooded, clay terra firme and white sand forests, which represent the range of resource availability, flooding and drought stress, forest structure, and floristic composition found throughout lowland Amazonian forests (Sobrado, 2009; Fine *et al.*, 2010; Baraloto *et al.*, 2011; Fortunel *et al.*, 2012). We selected the 15 most abundant species in each habitat to test for contrasting dominant strategies across habitats, and also selected species from seven monophyletic lineages that included species occurring in multiple habitats to test for phylogenetic signal in wood strategies and how they related to habitat association.

We investigated the following questions.

- (1) How does wood specific gravity relate to different wood anatomical traits in branches and roots? We expect fiber, lumen and vessel fractions to be correlated to wood specific gravity, while parenchyma fraction can vary independently. We also expect wood anatomical traits pertaining to transport to be related between branches and roots, while wood anatomical traits pertaining to support and storage are predicted to vary independently between branches and roots.
- (2) Do wood specific gravity and anatomy show concomitant variations across habitat types? We predict anatomical traits related to transport to vary between habitats according to changes in soil water availability. Specifically, we predict that species in white sand forests would exhibit higher wood specific gravity, greater fiber and parenchyma fractions, but lower vessel fraction and hydraulic conductivity than species in terra firme and seasonally flooded forests. As water is available throughout the year in seasonally flooded forests, we also predict that species in these forests would exhibit even lighter wood, greater hydraulic conductivity, and lower fiber and parenchyma fractions than species in terra firme forests.
- (3) Does the high turnover of plant species among habitat types affect wood trait correlations? According to previous findings on evolutionary patterns in wood specific gravity, we expect wood anatomical traits to be conserved within tropical tree genera. We thus predict that changes in plant community composition across environmental gradients can be explained in part by strong environmental filters on wood traits.

## Materials and Methods

### Study sites

We sampled broad environmental gradients representative of lowland South American rainforests, drawing from a network of 35 modified 0.5-ha Gentry plots in French Guiana that covers the more commonly studied clay terra firme forests in addition to seasonally flooded forests and white sand forests (Baraloto *et al.*, 2011). In all plots we recorded taxonomic identity for all trees

> 2.5 cm diameter at 1.3 m height (DBH; diameter at breast height), standardizing taxonomy with vouchers referenced with the Missouri Botanical Garden Herbarium, and environmental factors describing climate, soil and forest structure. We selected six plots at two locations in French Guiana (Petite Montagne Tortue to the east, and Laussat to the west), with one plot per habitat per location, to represent the variation in environmental conditions and floristic composition in the French Guianan network (Fortunel *et al.*, 2012). Annual average of measurements of soil water availability in the three studied plots in Laussat showed decreasing soil humidity from seasonally flooded forest (40%) to terra firme forest (17.5%) and finally to white sand forest (5.5%).

### Trait sampling

The aim of our study was not to investigate within-species variability in wood strategies, but instead to test for differences in wood strategies across habitats, accounting for species evolutionary history. Previous work showed that, to represent community-level trait distributions in species-rich plant communities, trait sampling can be achieved with only one individual of each species in each plot (Baraloto *et al.*, 2010a). Therefore, our sampling design was chosen so as to capture dominant wood strategies in each habitat by sampling the most abundant species, as well as to evaluate phylogenetic constraints on wood strategies by sampling representative species from focal monophyletic lineages.

To test for contrasting dominant strategies across habitats, we first selected the 15 most abundant species per plot. Pooling together the two studied plots per habitat type to calculate the percentage of the total abundance represented by the 15 most abundant species in each habitat, our sampling covered 24.6, 19.1 and 47.2% of the total abundance in seasonally flooded, terra firme and white sand forests, respectively. To test for phylogenetic signal in wood strategies, we additionally selected all species belonging to seven monophyletic lineages that are widespread across lowland Amazonian forests (Fine & Kembel, 2011) and that included species occurring in the three studied habitats: *Eschweilera* (Lecythidaceae), *Inga* (Fabaceae/Mimosaceae), *Licania* (Chrysobalanaceae), *Micropholis* (Sapotaceae), Bombacoideae (Malvaceae), *Protium* (Bursaceae) and *Swartzia* (Fabaceae/Papilionaceae). These lineages are phylogenetically dispersed within the eudicots, the dominant angiosperms in tropical rain forests, with representatives of euasterids (Sapotaceae), fabids (Fabaceae), and malvids (Malvaceae and Bursaceae). The selected phylogenetic lineages differ in their putative fossil-calibrated ages, with *Inga* spreading across the Amazon basin within the last few million years, *Swartzia* of intermediate age (10–19 million yr), and Bombacoideae (*Pachira*) and *Protium* likely to have longer histories (25–50 million yr) (Baum, 1995; Richardson *et al.*, 2001; Torke & Schaal, 2008).

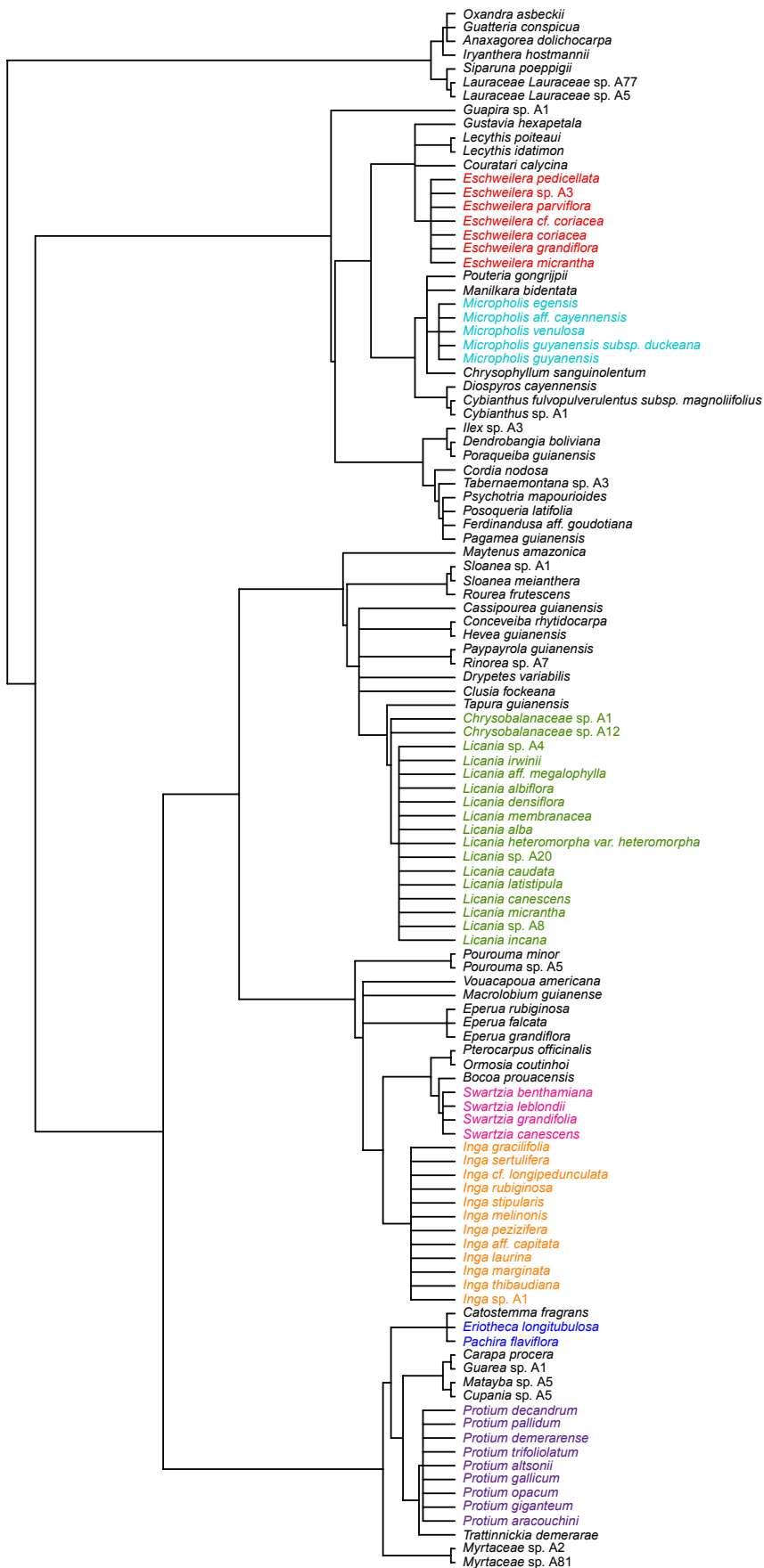
We measured wood traits on at least one individual per focal species in each plot (27 species were measured more than once), representing a total of 147 individuals and 113 species across the six plots (Fig. 1). For each species in each plot, we chose the stem nearest to 5 cm DBH, to standardize trait measures for the

majority of taxa to understorey light conditions and the small tree stage. We collected branch and small woody root samples for each selected individual during the dry season, between July 2009 and November 2009. From a lateral branch in the understorey, we collected a branch fragment in the last growth unit with a diameter of 1–2 cm. We dug at the base of each tree to sample a woody root section with a diameter of 1–2 cm, to be able to compare its structure with that of the branch. We attempted to sample small woody roots within 50 cm of the main stem with a lateral direction of growth to control for tension wood in the tissue. Branch and small woody root fragments were cut into two pieces: one piece was used to measure wood specific gravity, and the other to determine anatomical traits.

For wood specific gravity measurements, outer bark was removed for branch and root wood samples. For branch samples, pith wider than 1 mm in diameter was also removed (pith was negligible in root tissue samples). Branch and root samples were saturated with water and saturated volume was estimated using the Sartorius density determination kit (Goettingen, Germany), which is based on the principle of water displacement. After measurement of the saturated volume, samples were dried at 103°C for 72 h and dry mass was determined. Branch and root wood specific gravity (Williamson & Wiemann, 2010) was measured as the dry mass divided by the saturated volume.

For anatomical trait measurements, we cut cross-sections (15–20 µm thick) for each branch and root wood sample with a rotary microtome (Leica RM2255; Leica Microsystems, Wetzlar, Germany). Cross-sections were bleached (for 1 min), rinsed with distilled water (for 1 min) and dipped in ethanol at 50% (for 1 min) before being stained for 15 min in Safranin O (95%, pure, high-purity biological stain; Acros Organics, Geel, Belgium) solution (2% w/v). Cross-sections were dehydrated in ethanol series at 50% (for 1 min), at 75% (for 3 min) and at 100% (for 5 min) and then they were dipped in solvent (Clearene; Labonord, Templemars, France) before mounting. Up to nine cross-sections per sample were embedded in Eukitt Mounting Medium (Electron Microscopy, Hatfield, PA, USA) for histological examination. We selected one cross-section per sample and used a digital camera (Canon EOS 500D; Canon Inc., Tokyo, Japan) mounted on a light microscope (Olympus BX60; Olympus Corporation, Tokyo, Japan) to shoot eight photographs in natural light with an APO ×20 lens that together covered most of the wood area of the selected cross-section for each sample.

For each of the eight photographs of each branch and small woody root sample, image analyses were conducted with IMAGEJ 1.43 software (<http://rsb.info.nih.gov/ij/>) to determine branch and root anatomical traits (see details in Table 1). Anatomical traits measured in the eight photographs of each branch and root sample were then averaged to determine individual values. Image contrast was tuned manually to specifically examine: (1) vessel elements, and (2) parenchyma and fiber elements. We characterized the relative fractions of wood elements in the transversal plan, semi-automatically for vessel elements and manually for other wood elements: parenchyma fraction (Fp), fiber fraction (Ff), mean proportion of cell wall in fibers (Fmfw), total fiber



**Fig. 1** Evolutionary relationships for the 113 tropical tree taxa studied in French Guiana. The cladogram is based on the Angiosperm Phylogeny Group (APG) III classification. Colors indicate our seven focal phylogenetic lineages (red, *Eschweilera*; yellow, *Inga*; green, *Licania*; cyan, *Micropholis*; blue, Bombacoideae (*Pachira*); purple, *Protium*; pink, *Swartzia*), while common species are indicated in black.

**Table 1** List of branch and small root wood traits<sup>a</sup> measured on 147 individuals, representing a total of 113 species

Trait	Abbreviation	Function	Unit	Branch			Root			Organ F
				Mean	SD	Range	Mean	SD	Range	
Wood specific gravity	Wsg	Mechanical strength, sap conduction	No unit	0.608	0.104	0.308; 0.822	0.611	0.142	0.244; 0.946	0.076 ns
Lumen fraction	Fl	Porosity	No unit	0.259	0.079	0.092; 0.494	0.321	0.106	0.113; 0.556	0.146 ns
Parenchyma fraction	Fp	Carbohydrate storage	No unit	0.139	0.065	0.006; 0.350	0.179	0.079	0.042; 0.403	1.771 ns
Fiber fraction	Ff	Mechanical strength	No unit	0.770	0.062	0.558; 0.905	0.709	0.096	0.444; 0.897	3.264 ns
Mean fiber wall fraction	Fmfw	Mechanical strength	No unit	0.850	0.143	0.557; 1.000	0.862	0.156	0.432; 1.000	2.804 ns
Total fiber wall fraction	Ftfw	Mechanical strength	No unit	0.657	0.134	0.313; 0.905	0.611	0.143	0.244; 0.880	0.129 ns
Vessel fraction	Fv	Sap conduction	No unit	0.092	0.029	0.034; 0.172	0.113	0.085	0.014; 0.407	0.619 ns
Mean vessel area	A	Sap conduction	$\mu\text{m}^2$	$1.931 \times 10^3$	$1.040 \times 10^3$	$0.339 \times 10^3$ ; $5.572 \times 10^3$	$3.312 \times 10^3$	$3.351 \times 10^3$	$0.382 \times 10^3$ ; $21.439 \times 10^3$	0.923 ns
Vessel density	N	Sap conduction	$n \mu\text{m}^{-2}$	$0.066 \times 10^{-3}$	$0.048 \times 10^{-3}$	$0.012 \times 10^{-3}$ ; $0.345 \times 10^{-3}$	$0.051 \times 10^{-3}$	$0.046 \times 10^{-3}$	$0.007 \times 10^{-3}$ ; $0.299 \times 10^{-3}$	0.102 ns
Vessel lumen fraction	F	Sap conduction	No unit	0.092	0.029	0.035; 0.172	0.113	0.085	0.014; 0.407	0.619 ns
Vessel size to number ratio	S	Sap conduction	$\mu\text{m}^4$	$64.802 \times 10^6$	$77.687 \times 10^6$	$1.037 \times 10^6$ ; $418.517 \times 10^6$	$184.709 \times 10^6$	$342.015 \times 10^6$	$2.007 \times 10^6$ ; $2872.238 \times 10^6$	1.809 ns
Vessel mean hydraulic diameter	Dmh	Sap conduction	$\mu\text{m}^2$	50.117	13.756	20.897; 86.789	62.605	27.754	22.248; 174.050	0.473 ns
Conductivity index	lk	Sap conduction	$n \mu\text{m}^2$	352.661	224.481	57.419; 1236.012	1079.062	1888.830	9.863; 10232.107	1.360 ns
Specific xylem hydraulic conductivity	Ks	Sap conduction	$\text{kg s}^{-1} \text{MPa}^{-1}$	$4.310 \times 10^6$	$2.761 \times 10^6$	$0.522 \times 10^6$ ; $13.048 \times 10^6$	$11.237 \times 10^6$	$19.155 \times 10^6$	$0.143 \times 10^6$ ; $115.196 \times 10^6$	0.486 ns
Vessel group index	VGI	Sap conduction	No unit	$0.051 \times 10^{-3}$	$0.041 \times 10^{-3}$	$0.0004 \times 10^{-3}$ ; $0.3096 \times 10^{-3}$	$0.039 \times 10^{-3}$	$0.036 \times 10^{-3}$	$0.005 \times 10^{-3}$ ; $0.240 \times 10^{-3}$	0.300 ns

<sup>a</sup>Differences between branch and small root traits ( $n = 147$ ) are indicated with  $F$  statistics and significance test. ns, nonsignificant.



**Table 2** Pairwise correlations<sup>a</sup> among species mean branch and small root wood traits ( $n = 113$ )

	Branch														
	WSG	Fl	Fp	Ff	Fmfw	Ftfw	Fv	A	N	F	S	Dmh	lk	Ks	VGI
Branch															
WSG		<b>-0.803</b>	<b>-0.430</b>	<b>0.579</b>	<b>0.622</b>	<b>0.725</b>	-0.131	-0.174	0.138	-0.131	-0.112	-0.180	-0.175	-0.154	0.190
Fl	<b>-0.844</b>		<b>0.530</b>	<b>-0.752</b>	<b>-0.713</b>	<b>-0.858</b>	0.180	0.164	-0.106	0.180	0.084	0.166	0.180	0.162	-0.153
Fp	<b>-0.492</b>	<b>0.608</b>		<b>-0.842</b>	-0.207	<b>-0.451</b>	-0.364	0.369	<b>-0.495</b>	-0.364	<b>0.426</b>	<b>0.373</b>	0.147	0.183	<b>-0.502</b>
Ff	<b>0.614</b>	<b>-0.767</b>	<b>-0.869</b>		<b>0.397</b>	<b>0.670</b>	-0.095	-0.343	0.275	-0.095	-0.282	-0.344	-0.308	-0.301	0.291
Fmfw	<b>0.681</b>	<b>-0.707</b>	-0.176	<b>0.363</b>		<b>0.931</b>	-0.158	-0.015	-0.020	-0.158	0.048	-0.031	-0.099	-0.106	0.027
Ftfw	<b>0.802</b>	<b>-0.871</b>	<b>-0.427</b>	<b>0.629</b>	<b>0.924</b>		-0.198	-0.137	0.069	-0.198	-0.053	-0.150	-0.198	-0.197	0.119
Fv	-0.158	0.164	-0.324	-0.063	-0.311	-0.278		-0.134	<b>0.559</b>	1.000	-0.370	-0.146	0.293	0.203	<b>0.541</b>
A	-0.200	0.194	0.303	-0.337	-0.035	-0.134	-0.111		<b>-0.860</b>	-0.134	<b>0.958</b>	<b>0.996</b>	<b>0.871</b>	<b>0.856</b>	<b>-0.805</b>
N	0.023	-0.001	<b>-0.368</b>	0.195	-0.182	-0.087	<b>0.558</b>	<b>-0.762</b>		<b>0.559</b>	<b>-0.923</b>	<b>-0.875</b>	<b>-0.549</b>	<b>-0.581</b>	<b>0.964</b>
F	-0.158	0.164	-0.324	-0.063	-0.311	-0.278	1.000	-0.111	<b>0.558</b>		-0.370	-0.146	0.293	0.203	<b>0.541</b>
S	-0.118	0.099	<b>0.362</b>	-0.281	0.070	-0.025	-0.297	<b>0.903</b>	<b>-0.781</b>	-0.297		<b>0.952</b>	<b>0.730</b>	<b>0.743</b>	<b>-0.867</b>
Dmh	-0.202	0.190	<b>0.320</b>	-0.336	-0.039	-0.135	-0.137	<b>0.992</b>	<b>-0.795</b>	-0.137	<b>0.894</b>		<b>0.866</b>	<b>0.856</b>	<b>-0.823</b>
lk	-0.205	0.186	0.125	-0.282	-0.092	-0.173	0.220	<b>0.888</b>	<b>-0.521</b>	0.220	<b>0.709</b>	<b>0.879</b>		<b>0.934</b>	<b>-0.502</b>
Ks	-0.270	0.243	0.115	-0.265	-0.164	-0.225	0.193	<b>0.865</b>	<b>-0.506</b>	0.193	<b>0.699</b>	<b>0.862</b>	<b>0.954</b>		<b>-0.521</b>
VGI	0.062	-0.035	<b>-0.362</b>	0.189	-0.116	-0.034	<b>0.532</b>	<b>-0.717</b>	<b>0.951</b>	<b>0.532</b>	<b>-0.739</b>	<b>-0.749</b>	<b>-0.477</b>	<b>-0.466</b>	
Root															
WSG	<b>0.437</b>	<b>-0.483</b>	-0.164	<b>0.345</b>	<b>0.448</b>	<b>0.509</b>	-0.266	-0.141	-0.043	-0.266	-0.023	-0.134	-0.180	-0.221	-0.043
Fl	<b>-0.496</b>	<b>0.486</b>	0.233	<b>-0.339</b>	<b>-0.396</b>	<b>-0.473</b>	0.245	0.055	0.127	0.245	-0.043	0.059	0.093	0.138	0.084
Fp	-0.167	0.190	<b>0.378</b>	-0.363	0.017	-0.102	-0.068	0.336	-0.251	-0.068	0.320	0.330	0.291	0.227	-0.281
Ff	0.211	-0.193	-0.199	0.287	0.094	0.200	-0.207	-0.113	-0.024	-0.207	-0.041	-0.107	-0.112	-0.094	-0.011
Fmfw	<b>0.537</b>	<b>-0.532</b>	-0.039	0.177	<b>0.779</b>	<b>0.691</b>	-0.296	0.018	-0.224	-0.296	0.140	0.006	-0.035	-0.121	-0.149
Ftfw	<b>0.558</b>	<b>-0.545</b>	-0.160	0.324	<b>0.638</b>	<b>0.633</b>	-0.373	-0.085	-0.161	-0.373	0.038	-0.093	-0.149	-0.213	-0.118
Fv	-0.132	0.075	-0.121	-0.052	-0.160	-0.190	<b>0.428</b>	-0.137	0.321	<b>0.428</b>	-0.204	-0.147	-0.040	-0.012	0.325
A	0.013	-0.008	0.058	-0.116	0.036	0.009	-0.014	<b>0.372</b>	<b>-0.334</b>	-0.014	<b>0.312</b>	<b>0.388</b>	<b>0.288</b>	0.324	<b>-0.296</b>
N	-0.100	0.084	-0.184	0.074	-0.208	-0.184	0.415	<b>-0.535</b>	<b>0.680</b>	0.415	<b>-0.521</b>	<b>-0.564</b>	<b>-0.337</b>	-0.349	<b>0.622</b>
F	-0.132	0.075	-0.121	-0.052	-0.160	-0.190	<b>0.428</b>	-0.137	0.321	<b>0.428</b>	-0.204	-0.147	-0.040	-0.012	0.325
S	0.064	-0.032	0.076	-0.077	0.097	0.072	-0.168	<b>0.474</b>	<b>-0.497</b>	-0.168	<b>0.414</b>	<b>0.499</b>	<b>0.357</b>	<b>0.393</b>	<b>-0.441</b>
Dmh	0.012	-0.008	0.056	-0.110	0.040	0.016	-0.035	<b>0.383</b>	<b>-0.362</b>	-0.035	<b>0.313</b>	<b>0.404</b>	<b>0.300</b>	0.338	<b>-0.329</b>
lk	-0.086	0.056	0.027	-0.127	-0.035	-0.098	0.184	0.188	-0.070	0.184	0.135	0.192	0.171	0.205	-0.045
Ks	-0.066	0.050	0.015	-0.133	-0.065	-0.095	0.228	0.176	-0.056	0.228	0.102	0.187	0.172	0.220	-0.031
VGI	-0.057	0.054	-0.189	0.069	-0.163	-0.150	0.414	<b>-0.500</b>	<b>0.656</b>	0.414	<b>-0.471</b>	<b>-0.533</b>	<b>-0.304</b>	-0.324	<b>0.649</b>

<sup>a</sup>Spearman correlations coefficients for species data (above diagonal) and phylogenetically independent contrasts (below diagonal) are shown in bold type when significant, following Bonferroni-corrected alpha values ( $P < 5.37 \times 10^{-5}$ ). See Table 1 for trait abbreviations.

wall fraction ( $F_{tfw} = F_f \times F_{mfw}$ ), and vessel fraction ( $F_v$ ); as well as total (i.e. of all wood tissues) lumen fraction ( $Fl$ ) as an indicator of wood porosity. We determined vessel size ( $A$ , vessel mean area;  $D_1$ , vessel mean major diameter;  $D_2$ , vessel mean minor diameter), vessel density ( $N$ , vessel number per unit area) and vessel grouping index ( $GI$ , number of groups of vessels divided by vessel number) as defined by International Association of Wood Anatomists (Angyalossy Alfonso *et al.*, 1989). We calculated two metrics of vascular strategy related to xylem specific conductivity: vessel lumen fraction ( $F = A \times N$ : total cross-sectional area used for sap transport) and vessel size to number ratio ( $S = A/N$ ) (Zanne *et al.*, 2010). We computed hydraulic-related variables from vessel morphometric features. We calculated the mean hydraulic diameter as:  $D_{mh} = \sqrt[4]{\sum (2 D_1^2 D_2^2 / D_1^2 + D_2^2) / n}$ , where  $n$  is the number of vessels. We used the Poiseuille law to estimate the conductivity index as:  $I_k = N \times D_{mh}^4$ . We also used the Hagen–Poiseuille equation to calculate the theoretical specific xylem hydraulic conductivity as:  $Ks = (\pi / 128 \eta A_{cross\ section}) \times \sum D_1^2 D_2^2$ , where  $\eta$  is water viscosity ( $1.002 \times 10^{-9}$  MPa s<sup>-1</sup> at 20°C) (Tyree & Ewers, 1991).

## Data analysis

The first step of our analysis was to investigate how wood specific gravity relates to different wood anatomical traits in branches and roots. Data were not transformed for the sake of better interpretability and comparison with other studies, so we used nonparametric tests.

To examine the trait-by-trait correlations among traits defining branch and small woody root tissues, we performed pairwise Spearman correlation tests between (1) species means ( $n = 113$ ), and (2) individual values ( $n = 147$ ) using the mean value of each trait for each of the 113 studied species. As correlation tests are sensitive to missing data, we used the trait means from the closest taxonomic level (genus or family) when branch or root data were missing ( $n = 12$  and 25, respectively).

We further examined the influence of species evolutionary histories on the observed correlations between groups of traits by performing pairwise correlations between species mean traits ( $n = 113$ ) including phylogenetically independent contrasts (PICs). We recovered a phylogenetic tree for our 113 species using the PHYLOMATIC v.3 utility (Webb & Donoghue, 2005),

Root														
WGS	Fl	Fp	Ff	Fmfw	Ftfw	Fv	A	N	F	S	Dmh	lk	Ks	VGI
0.479	-0.529	-0.245	0.266	0.493	0.551	-0.077	-0.052	0.053	-0.077	-0.074	-0.048	-0.078	-0.050	0.098
-0.497	0.505	0.199	-0.206	-0.509	-0.528	0.028	-0.033	-0.025	0.028	-0.016	-0.019	-0.007	-0.028	-0.051
-0.264	0.234	0.424	-0.243	-0.017	-0.147	-0.140	0.148	-0.288	-0.140	0.256	0.147	0.024	0.020	-0.297
0.431	-0.379	-0.364	0.333	0.203	0.341	-0.056	-0.153	0.137	-0.056	-0.170	-0.160	-0.133	-0.121	0.149
0.483	-0.427	-0.020	0.112	0.685	0.581	-0.061	-0.005	-0.018	-0.061	0.004	-0.009	-0.027	-0.018	0.028
0.544	-0.498	-0.125	0.217	0.625	0.603	-0.101	-0.063	0.017	-0.101	-0.047	-0.071	-0.092	-0.077	0.060
-0.152	0.208	-0.130	-0.142	-0.236	-0.281	0.388	-0.034	0.370	0.388	-0.228	-0.026	0.203	0.182	0.366
-0.187	0.042	0.260	-0.080	0.063	0.015	-0.148	0.432	-0.564	-0.148	0.568	0.438	0.177	0.199	-0.538
0.127	-0.022	-0.307	0.068	-0.100	-0.060	0.257	-0.401	0.625	0.257	-0.585	-0.398	-0.097	-0.115	0.617
-0.152	0.208	-0.130	-0.142	-0.236	-0.281	0.388	-0.034	0.370	0.388	-0.228	-0.026	0.203	0.182	0.366
-0.110	-0.043	0.254	-0.012	0.131	0.109	-0.239	0.414	-0.619	-0.239	0.592	0.418	0.108	0.139	-0.590
-0.193	0.070	0.279	-0.106	0.035	-0.016	-0.143	0.445	-0.570	-0.143	0.580	0.452	0.190	0.211	-0.548
-0.233	0.111	0.176	-0.108	-0.040	-0.085	-0.004	0.375	-0.384	-0.004	0.441	0.388	0.231	0.237	-0.364
-0.186	0.112	0.198	-0.123	-0.076	-0.102	-0.008	0.319	-0.339	-0.008	0.394	0.330	0.199	0.217	-0.314
0.145	-0.090	-0.326	0.090	-0.039	0.002	0.229	-0.390	0.594	0.229	-0.550	-0.391	-0.104	-0.117	0.624
	-0.684	-0.259	0.466	0.442	0.631	-0.272	-0.386	0.185	-0.272	-0.348	-0.379	-0.362	-0.370	0.242
-0.689		0.417	-0.682	-0.534	-0.830	0.362	0.307	-0.066	0.362	0.243	0.315	0.374	0.344	-0.152
-0.096	0.372		-0.615	0.018	-0.291	-0.260	0.176	-0.381	-0.260	0.355	0.173	-0.017	0.012	-0.423
0.489	-0.732	-0.519		0.131	0.619	-0.518	-0.499	0.023	-0.518	-0.327	-0.504	-0.609	-0.586	0.094
0.431	-0.482	0.043	0.103		0.817	-0.149	-0.019	-0.075	-0.149	0.032	-0.023	-0.092	-0.073	-0.021
0.617	-0.808	-0.239	0.576	0.793		-0.396	-0.284	-0.006	-0.396	-0.164	-0.295	-0.389	-0.363	0.073
-0.459	0.490	-0.250	-0.587	-0.230	-0.488		0.436	0.458	1.000	-0.003	0.444	0.826	0.759	0.394
-0.421	0.290	0.024	-0.416	0.003	-0.261	0.427		-0.524	0.436	0.865	0.993	0.840	0.867	-0.556
0.014	0.099	-0.271	-0.034	-0.225	-0.133	0.363	-0.520		0.458	-0.830	-0.525	-0.028	-0.114	0.973
-0.459	0.490	-0.250	-0.587	-0.230	-0.488	1.000	0.427	0.363		-0.003	0.444	0.826	0.759	0.394
-0.303	0.213	0.165	-0.256	0.030	-0.165	0.080	0.835	-0.737	0.080		0.849	0.496	0.563	-0.836
-0.404	0.291	0.022	-0.408	0.013	-0.254	0.405	0.981	-0.551	0.405	0.819		0.839	0.863	-0.557
-0.470	0.431	-0.051	-0.588	-0.070	-0.392	0.741	0.846	-0.152	0.741	0.567	0.803		0.974	-0.081
-0.467	0.391	-0.076	-0.539	-0.109	-0.408	0.700	0.863	-0.194	0.700	0.597	0.827	0.958		-0.168
0.056	0.030	-0.276	-0.007	-0.160	-0.077	0.338	-0.531	0.969	0.338	-0.733	-0.572	-0.166	-0.212	

based on the Davies *et al.* (2004) phylogenetic hypothesis for relationships among angiosperm families, with polytomies applied within most families and genera. For this analysis, branch lengths were scaled to 1. PICs were calculated as the difference in mean trait values for pairs of sister species and nodes (Coomes & Grubb, 1996).

To illustrate the correlations both within and among branch and root wood traits, we performed a principal components analysis (PCA) on species mean traits. We conducted this analysis both with and without the PICs to account for the influence of species evolutionary histories. Additionally, we tested for differences between branch and root traits using analysis of variance (ANOVA) with organ as an independent variable.

To test the generality of the correlation patterns between branch and root wood traits across the three contrasting habitats, we performed a PCA on individual traits measured in each plot and performed Mantel tests for similarity of pairwise trait correlation matrices among the six plots.

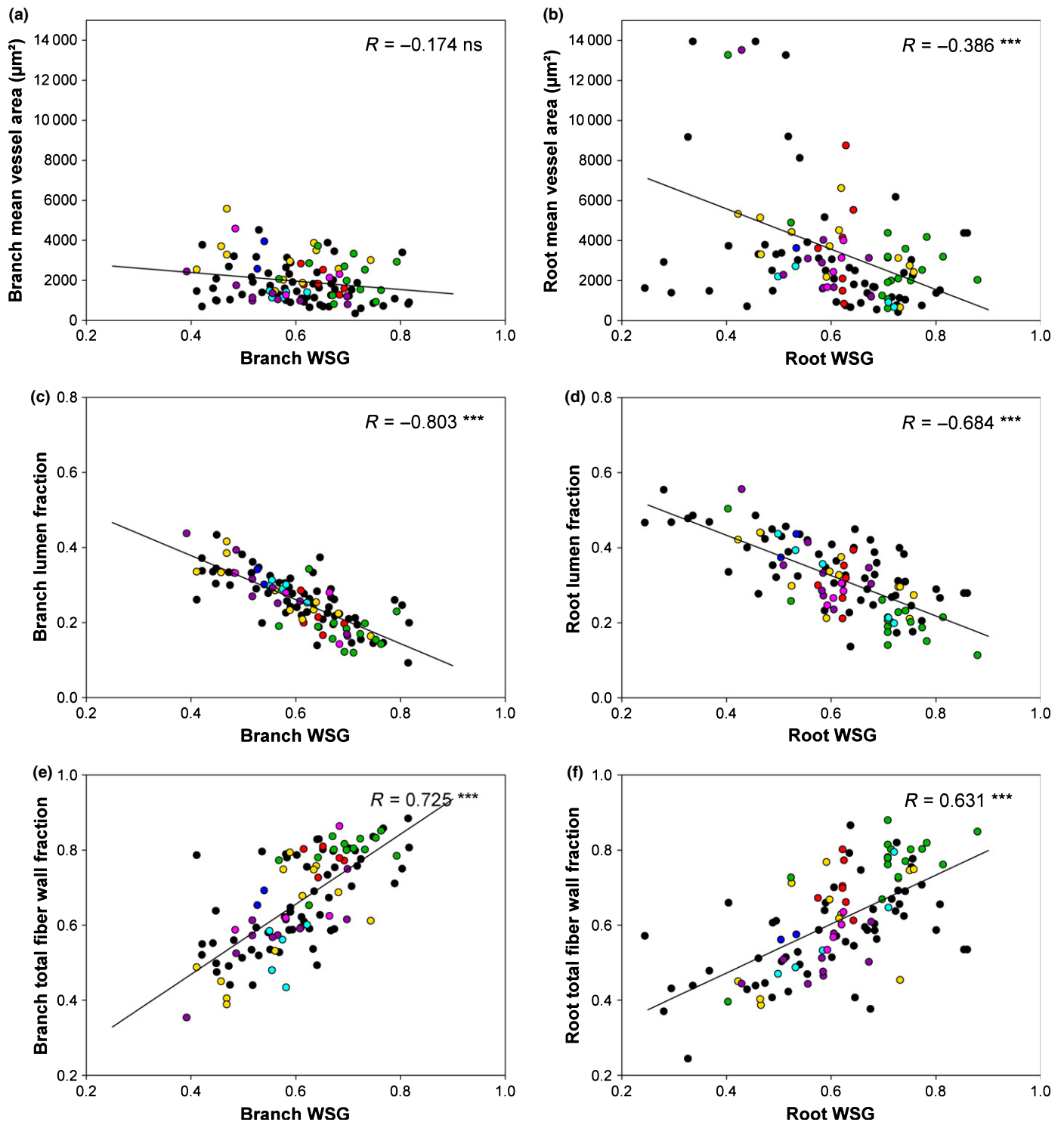
The second step of our analysis was to examine how wood specific gravity and anatomy vary between habitats as well as between species. We conducted two-way ANOVA to examine

the effect of habitat and lineage (15 most abundant species and seven focal monophyletic lineages) on individual values of wood specific gravity and anatomy in branches and roots. When necessary, we performed *post hoc* tests (Tukey's HSD test) to identify variation among habitats or lineages.

All analyses were conducted in the R 2.15.3 statistical platform (R Development Core Team, 2011), using the packages ADE4 (Ellers *et al.*, 2011), APE (Coomes & Grubb, 1996) and VEGAN (Dixon, 2003).

## Results

Pairwise correlations between species mean traits showed that wood specific gravity was strongly correlated between branches and roots (Table 2). We found strong patterns of coordination among branch traits, with species exhibiting high branch specific wood gravity also showing high fiber and fiber wall fractions but low lumen and parenchyma fractions, while branch vessel traits varied independently (Table 2, Fig. 2a,c,e). Species with high root specific wood gravity similarly had high fiber and fiber wall fractions but a low lumen fraction and small vessel size and vessel

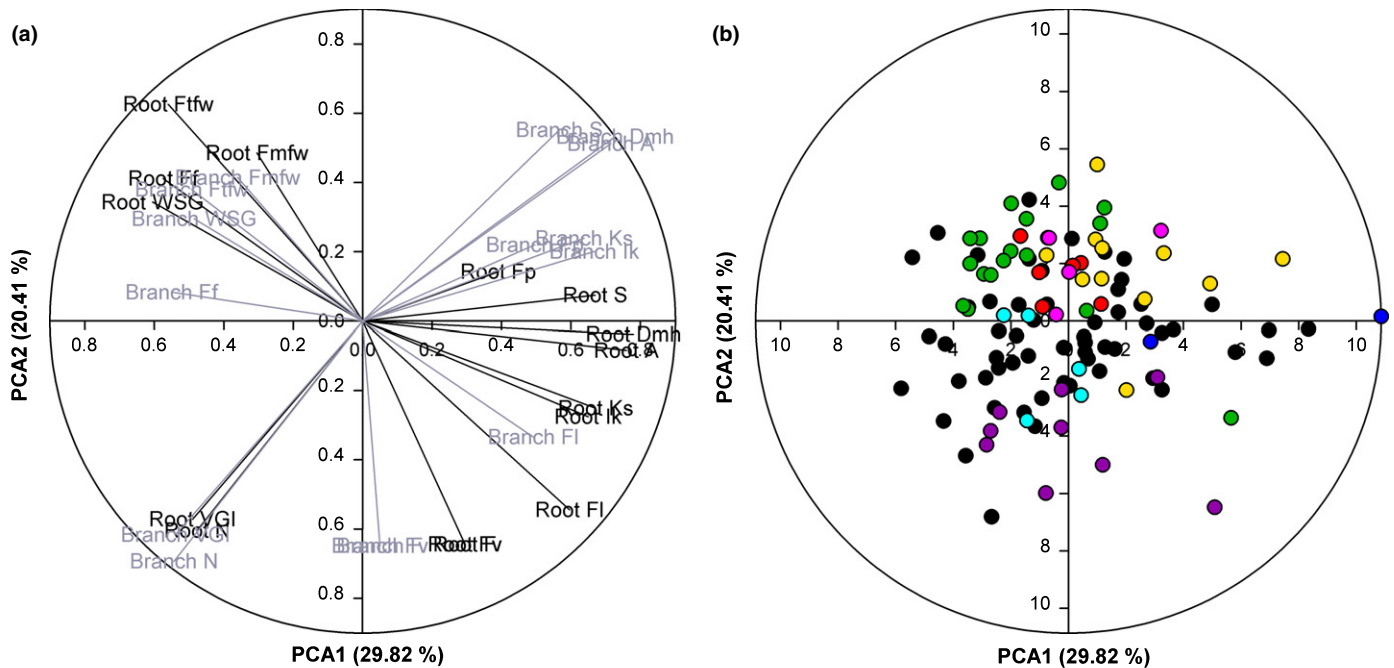


**Fig. 2** Relationships between wood specific gravity (WSG) and mean vessel area (a, b), lumen (c, d) and fiber wall (e, f) fractions in branches and small woody roots in 113 tropical tree species. Spearman correlation coefficients ( $R$ ) are given with significance test (\*\*\*,  $P < 0.001$ ; ns, nonsignificant). When correlations were significant both with and without including phylogenetically independent contrasts, ordinary least-squares regression lines were drawn. Colors indicate our seven focal phylogenetic lineages (red, *Eschweilera*; yellow, *Inga*; green, *Licania*; cyan, *Micropholis*; blue, Bombacoideae (*Pachira*); purple, *Protium*; pink, *Swartzia*), while common species are indicated in black.

mean hydraulic diameter (Table 2, Fig. 2b,d,f). The matrices of pairwise trait correlations between species means and between individual values showed similar patterns ( $R_{\text{Mantel}} = 0.99$ ;  $P < 0.0001$ ).

When PICs were included in the pairwise correlations between species mean traits, the patterns of correlations among branch and root wood traits were generally conserved (Table 2). The matrices of pairwise correlations between species mean traits





**Fig. 3** Principal components analysis (PCA) on branch and small woody root wood trait means in 113 tropical tree species: (a) correlation circle of data and (b) individual factor map of data without phylogenetically independent contrasts. In (a), stem wood traits are shown in gray, while root wood traits are shown in black. In (b), colors indicate our seven focal phylogenetic lineages (red, *Eschweilera*; yellow, *Inga*; green, *Licania*; cyan, *Micropholis*; blue, Bombacoideae (*Pachira*); purple, *Protium*; pink, *Swartzia*), while common species are indicated in black. See Table 1 for trait abbreviations.

determined with and without PICs were similar ( $R_{\text{Mantel}} = 0.98$ ;  $P < 0.0001$ ). Hence there seems to be no effect of species evolutionary history on the correlation patterns among traits related to branch and root wood tissues.

The multivariate analysis of trait correlations showed that branch and woody root traits defined three major axes (Fig. 3a). The first PCA axis (29.82%) was defined by coordinated branch and woody root vessel traits, opposing wood with large vessels, in terms of area and hydraulic diameter, and vessel size to number ratio against wood with high vessel density and high vessel grouping index. The second axis of the PCA (20.41%) was defined by coordinated root wood traits related to tissue structure, opposing wood with high root specific wood gravity and fiber and fiber wall fractions against wood with high root lumen and vessel fractions as well as a high root vessel lumen fraction. The third axis of the PCA (15.80%) was defined by coordinated branch wood traits related to tissue structure, opposing wood with high branch specific wood gravity and fiber and fiber wall fractions against wood with a high branch lumen fraction.

When PICs were included in the PCA, the patterns of correlations among branch and root wood traits were consistent (Table 2), further confirming that phylogeny was not a strong predictor of the observed patterns between branch and root wood traits. Moreover, we found no differences between branch and root wood anatomical traits (Table 1).

The matrices of pairwise correlations between branch and woody root traits were similar among the six plots representing the steep gradient of environmental conditions found in French Guiana (Supporting Information Table S1). The generality of coordination patterns of branch and woody root traits was

supported by the consistency of the three PCA axes along broad environmental gradients.

Species in white sand plots exhibited higher wood specific gravity of both branches and roots than those in terra firme and seasonally flooded plots; whereas species in terra firme had higher wood specific gravity of both branches and roots than those in seasonally flooded plots (Table 3, Fig. 4a,b). Similarly, species in white sand plots exhibited higher branch fiber, mean fiber wall and total fiber fractions, but lower branch and root parenchyma fractions and branch lumen fraction than those in seasonally flooded plots (Fig. 4c–f; see Fig. S1 for complete results). However, most anatomical traits related to vessels did not vary among the three habitats (Table 3, Fig. S1).

We found a strong effect of lineage on branch specific wood gravity as well as on branch and woody root anatomy, with significant differences among phylogenetic lineages for all traits, but without any interactions with habitat for most traits (Table 3, Figs 3b, 4; see Fig. S2 for complete results). For instance, *Licania* species exhibited higher branch specific wood gravity (Fig. 5a) as well as higher branch and root fiber and fiber wall fractions (Fig. 5e,f) but lower branch and root lumen fractions (Fig. 5c,d) than species from other lineages. *Protium* species had higher vessel fraction and vessel grouping in branches and roots than most other lineages (Fig. S2). *Inga* species exhibited higher branch vessel size, but lower branch vessel density than most *Micropholis*, *Protium* and common species (Fig. S2). Bombacoideae (*Pachira*) species had higher vessel size and vessel mean hydraulic diameter in roots than most *Micropholis* species (Fig. S2). In general, congeneric species had very similar values across different habitat types, and we found that the proportion of variance explained by

**Table 3** Influence of habitat, lineage and their interaction on branch and small root wood traits ( $n = 147$ )

Trait	Habitat			Lineage			Common species	<i>Eschweilera</i>		
	$\omega^2$	<i>F</i>	Seasonally flooded	Terra firme	White sand	$\omega^2$			<i>F</i>	
Branch	WSG	35.73	13.41***	0.562 bc	0.604 b	0.665 a	33.13	4.29***	0.604 b	0.643 b
	Fl	13.11	5.13**	0.285 b	0.254 ab	0.237 a	37.54	4.38***	0.265 a	0.214 ab
	Fp	22.50	6.42**	0.162 a	0.138 ab	0.114 b	19.33	2.40*	0.139 ab	0.161 ab
	Ff	16.36	5.52**	0.748 b	0.773 ab	0.789 a	25.37	3.00**	0.770 a	0.766 ab
	Fmfw	14.03	8.58***	0.806 b	0.843 ab	0.908 a	56.62	9.74***	0.843 b	0.945 ab
	Ftfw	19.45	11.06***	0.605 b	0.656 ab	0.716 a	42.63	7.30***	0.652 b	0.727 ab
	Fv	1.63	1.48 ns	0.090 a	0.089 a	0.098 a	57.13	5.80***	0.091 b	0.073 b
	A	2.94	1.72 ns	$2.133 \times 10^3$ a	$1.899 \times 10^3$ a	$1.747 \times 10^3$ a	53.66	4.75***	$1.762 \times 10^3$ b	$1.827 \times 10^3$ ab
	N	8.47	2.83†	$0.055 \times 10^{-3}$ a	$0.067 \times 10^{-3}$ a	$0.078 \times 10^{-3}$ a	49.58	4.06***	$0.071 \times 10^{-3}$ a	$0.043 \times 10^{-3}$ ab
	F	1.63	1.48 ns	0.090 a	0.089 a	0.098 a	57.13	5.80***	0.091 b	0.073 b
	S	0.34	0.92 ns	$75.254 \times 10^6$ a	$64.340 \times 10^6$ a	$53.632 \times 10^6$ a	62.49	5.10***	$51.585 \times 10^6$ b	$51.543 \times 10^6$ b
	Dmh	4.74	2.29 ns	53.195 a	49.553 a	47.438 a	55.94	5.34***	47.619 b	49.813 ab
	lk	0.38	1.08 ns	391.250 a	333.592 a	336.093 a	24.86	2.54*	322.890 b	279.867 ab
	Ks	5.26	2.22 ns	$4.977 \times 10^6$ a	$4.063 \times 10^6$ a	$3.906 \times 10^6$ a	24.45	2.62*	$3.892 \times 10^6$ a	$2.962 \times 10^6$ a
	VGI	7.78	2.60†	$0.041 \times 10^{-3}$ a	$0.053 \times 10^{-3}$ a	$0.060 \times 10^{-3}$ a	45.88	3.70**	$0.053 \times 10^{-3}$ ab	$0.032 \times 10^{-3}$ b
Root	WSG	41.93	9.43***	0.542 b	0.616 a	0.676 a	9.48	1.55 ns	0.596 a	0.622 a
	Fl	3.81	2.43†	0.349 a	0.311 a	0.308 a	45.42	5.86***	0.352 ab	0.303 ab
	Fp	12.12	3.36*	0.195 a	0.185 ab	0.151 b	50.49	3.81**	0.191 a	0.203 ab
	Ff	1.14	0.77 ns	0.708 a	0.699 a	0.724 a	50.50	3.90***	0.704 ab	0.699 ab
	Fmfw	4.59	2.54†	0.820 a	0.872 a	0.889 a	63.59	7.10***	0.828 b	1.000 a
	Ftfw	3.58	2.33 ns	0.880 a	0.852 a	0.866 a	60.02	7.38***	0.866 a	0.802 a
	Fv	0.75	1.19 ns	0.097 a	0.115 a	0.125 a	58.56	5.06***	0.105 b	0.098 b
	A	2.15	0.38 ns	$3.464 \times 10^3$ a	$3.441 \times 10^3$ a	$2.923 \times 10^3$ a	19.76	2.63*	$2.931 \times 10^3$ b	$4.147 \times 10^3$ ab
	N	2.91	1.50 ns	$0.041 \times 10^{-3}$ a	$0.055 \times 10^{-3}$ a	$0.056 \times 10^{-3}$ a	54.20	3.66**	$0.057 \times 10^{-3}$ ab	$0.033 \times 10^{-3}$ b
	F	0.75	1.19 ns	0.097 a	0.115 a	0.125 a	58.56	5.06***	0.105 b	0.098 b
	S	2.16	2.60†	$203.195 \times 10^6$ a	$220.59 \times 10^6$ a	$102.811 \times 10^6$ a	20.86	5.40***	$155.791 \times 10^6$ b	$261.792 \times 10^6$ ab
	Dmh	4.13	0.15 ns	62.760 a	63.225 a	60.225 a	25.71	2.52*	58.072 ab	70.198 ab
	lk	3.69	0.13 ns	1099.217 a	1140.331 a	951.712 a	19.68	2.33*	855.030 b	1319.942 ab
	Ks	2.29	0.30 ns	$10.886 \times 10^6$ a	$12.419 \times 10^6$ a	$9.591 \times 10^6$ a	12.81	2.12*	$8.741 \times 10^6$ a	$13.963 \times 10^6$ a
	VGI	2.66	1.43 ns	$0.031 \times 10^{-3}$	$0.042 \times 10^{-3}$	$0.043 \times 10^{-3}$	54.17	3.50**	$0.042 \times 10^{-3}$ b	$0.024 \times 10^{-3}$ b

Proportions of variance explained by each factor ( $\omega^2$ ) are indicated; *F* statistics are shown with significance test (†,  $0.05 < P < 0.07$ ; \*,  $P < 0.05$ ; \*\*,  $P < 0.01$ ; \*\*\*,  $P < 0.001$ ; ns, nonsignificant). Means for each habitat and lineage are indicated with *post hoc* Tukey's HSD (Honestly Significant Difference) test in bold letters. See Table 1 for trait abbreviations.

habitat type was lower than the proportion of variance explained by lineage for most anatomical traits (Table 3).

## Discussion

### Relationships among wood specific gravity and wood anatomy in branches and roots

Our study helps to reveal how wood anatomical traits contribute to wood specific gravity in both aboveground and belowground woody systems of tree species across broad environmental gradients in lowland Amazonian forests. Our hypotheses were that wood specific gravity would decrease with increasing vessel fraction (Preston *et al.*, 2006), but increase with increasing fiber fraction (Poorter *et al.*, 2010). We measured 15 branch and small woody root wood traits pertaining to conduction, support and storage functions in 147 individuals representing 113 species across three contrasting habitats in French Guiana. We found that increases in wood specific gravity of both branches and roots of tropical tree species were largely driven by decreasing lumen fraction and increasing fiber and fiber wall fractions, regardless of

variations in vessel and parenchyma fractions. Thus, wood specific gravity of both branches and roots of tropical tree species mostly depends on the cell wall thickness of fibers, as found in previous studies including all wood anatomical elements of stems or roots in Mediterranean, temperate and tropical species (Jacobsen *et al.*, 2007a; Pratt *et al.*, 2007; Martinez-Cabrera *et al.*, 2009; Schuldt *et al.*, 2013). Previous findings linked increasing wood mechanical strength with increasing cavitation resistance: mechanical reinforcement of vessels by the neighboring fiber matrix can indeed play an important role in avoiding vessel collapse under negative pressure (Hacke *et al.*, 2001; Jacobsen *et al.*, 2005, 2007b; Pratt *et al.*, 2007; Lens *et al.*, 2011).

At the organ level, we observed that branches and roots differed in how wood specific gravity related to anatomical wood traits involved in sap transport. Contrary to our expectation, we found no relationship between wood specific gravity and vascular traits at the branch level, suggesting no tradeoff between wood specific gravity and conduction capacity in branches. Our results differ from those of previous studies conducted at relatively small spatial scales that showed that stem wood specific gravity related to vessel and vessel lumen fractions (Baltzer *et al.*, 2009; Gleason

Inga	Licania	Micropholis	Bombacoideae			Habitat × lineage	
			(Pachira)	Protium	Swartzia	$\omega^2$	F
0.589 b	0.702 a	0.578 b	0.530 b	0.556 b	0.624 b	0.54	0.97 ns
0.263 ab	0.185 b	0.287 a	0.331 a	0.292 a	0.265 ab	14.42	1.76 <sup>†</sup>
0.156 ab	0.116 b	0.114 b	0.228 a	0.117 b	0.140 ab	14.93	1.63 <sup>†</sup>
0.771 ab	0.800 a	0.770 ab	0.663 b	0.761 ab	0.780 ab	18.48	1.85*
0.819 b	1.000 a	0.716 b	1.000 a	0.737 b	0.839 ab	8.98	1.81 <sup>†</sup>
0.636 b	0.800 a	0.552 b	0.663 ab	0.568 b	0.657 ab	16.66	2.44**
0.073 b	0.084 b	0.116 a	0.109 ab	0.122 a	0.079	3.85	1.19 ns
$2.838 \times 10^3$ a	$2.053 \times 10^3$ ab	$1.301 \times 10^3$ b	$2.919 \times 10^3$ ab	$1.359 \times 10^3$ b	$2.427 \times 10^3$ ab	1.57	0.94 ns
$0.031 \times 10^{-3}$ b	$0.069 \times 10^{-3}$ ab	$0.095 \times 10^{-3}$ a	$0.040 \times 10^{-3}$ ab	$0.104 \times 10^{-3}$ a	$0.041 \times 10^{-3}$ ab	9.03	0.68 ns
0.073 b	0.084 b	0.116 b	0.109 ab	0.122 a	0.079 b	3.85	1.19 ns
$145.293 \times 10^6$ a	$82.121 \times 10^6$ ab	$16.975 \times 10^6$ b	$90.035 \times 10^6$ ab	$20.682 \times 10^6$ b	$95.289 \times 10^6$ ab	10.01	0.62 ns
62.740 a	51.349 ab	42.439 b	63.818 a	42.138 b	57.035 ab	1.23	0.94 ns
442.668 ab	366.845 ab	296.371 ab	681.882 a	324.549 ab	390.799 ab	24.08	1.87*
$5.473 \times 10^6$ a	$4.756 \times 10^6$ a	$3.516 \times 10^6$ a	$7.686 \times 10^6$ a	$4.333 \times 10^6$ a	$4.887 \times 10^6$ a	22.71	1.87*
$0.026 \times 10^{-3}$ b	$0.064 \times 10^{-3}$ ab	$0.052 \times 10^{-3}$ ab	$0.029 \times 10^{-3}$ ab	$0.089 \times 10^{-3}$ a	$0.029 \times 10^{-3}$ b	7.13	0.76 ns
0.615 a	0.714 a	0.606 a	0.526 a	0.582 a	0.604 a	6.12	0.80 ns
0.327 ab	0.213 b	0.324 ab	0.421 a	0.346 ab	0.266 ab	21.37	2.33*
0.209 a	0.141 ab	0.142 ab	0.241 ab	0.116 b	0.226 ab	19.10	0.38 ns
0.686 ab	0.771 a	0.760 a	0.572 b	0.664 b	0.740 ab	4.07	0.86 ns
0.892 ab	0.989 a	0.746 b	1.000 a	0.761 b	0.767 b	0.94	0.95 ns
0.768 a	0.880 a	0.795 ab	0.651 ab	0.649 b	0.635 a	6.81	1.42 ns
0.104 b	0.088 b	0.098 b	0.188 b	0.221 a	0.033 b	4.62	0.81 ns
$4.519 \times 10^3$ ab	$3.059 \times 10^3$ ab	$1.658 \times 10^3$ b	$8.081 \times 10^3$ a	$3.131 \times 10^3$ ab	$2.428 \times 10^3$ ab	44.29	3.13***
$0.024 \times 10^{-3}$ b	$0.044 \times 10^{-3}$ b	$0.065 \times 10^{-3}$ ab	$0.045 \times 10^{-3}$ ab	$0.093 \times 10^{-3}$ a	$0.016 \times 10^{-3}$ b	21.14	0.40 ns
0.104 b	0.088 b	0.098 b	0.188 ab	0.221 a	0.033 b	4.62	0.81 ns
$285.182 \times 10^6$ ab	$153.744 \times 10^6$ b	$31.942 \times 10^6$ b	$782.428 \times 10^6$ a	$69.691 \times 10^6$ b	$213.367 \times 10^6$ ab	62.07	9.63***
76.037 ab	61.135 ab	46.227 b	96.727 a	61.353 ab	55.956 ab	25.26	1.87*
1374.050 ab	834.129 ab	412.433 b	3675.924 a	1842.556 ab	161.836 b	37.57	2.48**
$15.163 \times 10^6$ a	$9.554 \times 10^6$ a	$4.715 \times 10^6$ a	$33.955 \times 10^6$ a	$18.140 \times 10^6$ a	$2.335 \times 10^6$ a	53.34	3.71***
$0.019 \times 10^{-3}$ b	$0.039 \times 10^{-3}$ b	$0.041 \times 10^{-3}$ a	$0.032 \times 10^{-3}$ a	$0.076 \times 10^{-3}$ a	$0.011 \times 10^{-3}$ b	24.88	0.33 ns

*et al.*, 2012) and vascular traits (Ackerly, 2004; Preston *et al.*, 2006; Jacobsen *et al.*, 2007a; Martinez-Cabrera *et al.*, 2011; McCulloh *et al.*, 2011), but confirm those of recent studies conducted at transcontinental and global scales that found no such relationships between stem wood specific gravity and vascular traits (Martinez-Cabrera *et al.*, 2009; Poorter *et al.*, 2010; Russo *et al.*, 2010; Zanne *et al.*, 2010; Fan *et al.*, 2012). Yet we found significant negative correlations between wood specific gravity and mean vessel area and mean vessel hydraulic diameter in roots. This result suggests fundamental differences between aboveground and belowground xylem: fibers in branches perform the dual function of mechanical support and cavitation resistance, while vessels in roots may play a greater role in resisting cavitation, given that the soil matrix surrounding roots acts as mechanical support (Hacke & Sperry, 2001; Pratt *et al.*, 2007).

#### Associations among wood anatomical traits in branches and roots

In our large sample of tropical tree species, we found the expected correlation among anatomical wood traits pertaining

to sap transport across both branches and small woody roots, confirming the hypothesis of tight hydraulic continuity between belowground and aboveground compartments (Tyree & Ewers, 1991; Blonder *et al.*, 2011): wood with higher mean vessel area but lower vessel density, reflected by higher vessel size to number ratio, and with more grouped vessels, showed higher mean vessel hydraulic diameter, associated with higher estimated hydraulic conductivity. Our results also confirm the tradeoff between vessel size and density, which has been interpreted in other studies as a tradeoff between hydraulic efficiency and hydraulic safety: species with few large vessels, reflected by high vessel size to number ratio, tend to increase hydraulic conductivity, which has been related to increasing potential cavitation risk (Sperry *et al.*, 2006, 2008; Poorter *et al.*, 2010; Zanne *et al.*, 2010). Moreover, our estimates of hydraulic conductivity provide strong support for recent theoretical insights suggesting that higher vessel interconnectivity should increase hydraulic conductivity (Loepfe *et al.*, 2007; Jansen *et al.*, 2011; Martinez-Vilalta *et al.*, 2012). Grouped vessels indeed present a greater portion of walls in contact with neighboring vessels: they are

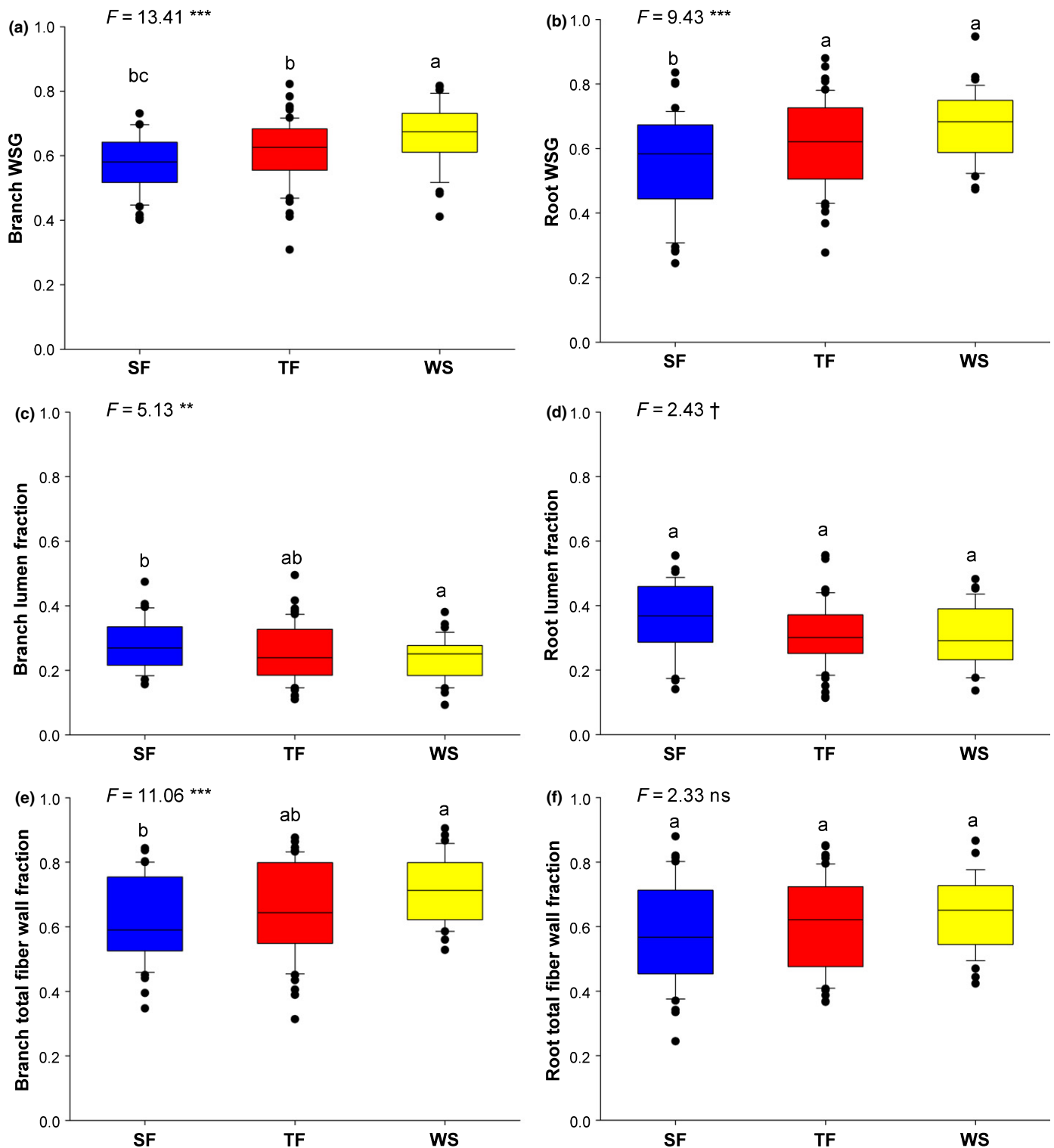


Fig. 4 Boxplots of branch and root (a, b) wood specific gravity, (c, d) lumen fraction and (e, f) total fiber wall fraction by habitat. The line in the box indicates the median; the whiskers above and below the box indicate the 90th and 10th percentiles.  $F$  statistics are shown with significance test (†,  $0.05 < P < 0.07$ ; \*,  $P < 0.05$ ; \*\*,  $P < 0.01$ ; \*\*\*,  $P < 0.001$ ; ns, nonsignificant); *post hoc* Tukey's HSD (Honestly Significant Difference) test is indicated in bold letters. Colors indicate our three habitats (blue, seasonally flooded forest; red, terra firme forest; yellow, white sand forest). SF, seasonally flooded forest; TF, terra firme forest; WS, white sand forest. See Table 1 for trait abbreviations.

therefore connected by many inter-vessel pits that allow a high hydraulic conductivity although an increased cavitation risk. To our knowledge, only one other study, on the genus

*Acer*, has so far shown the importance of vessel grouping on hydraulic conductivity and associated embolism risk (Lens *et al.*, 2011).

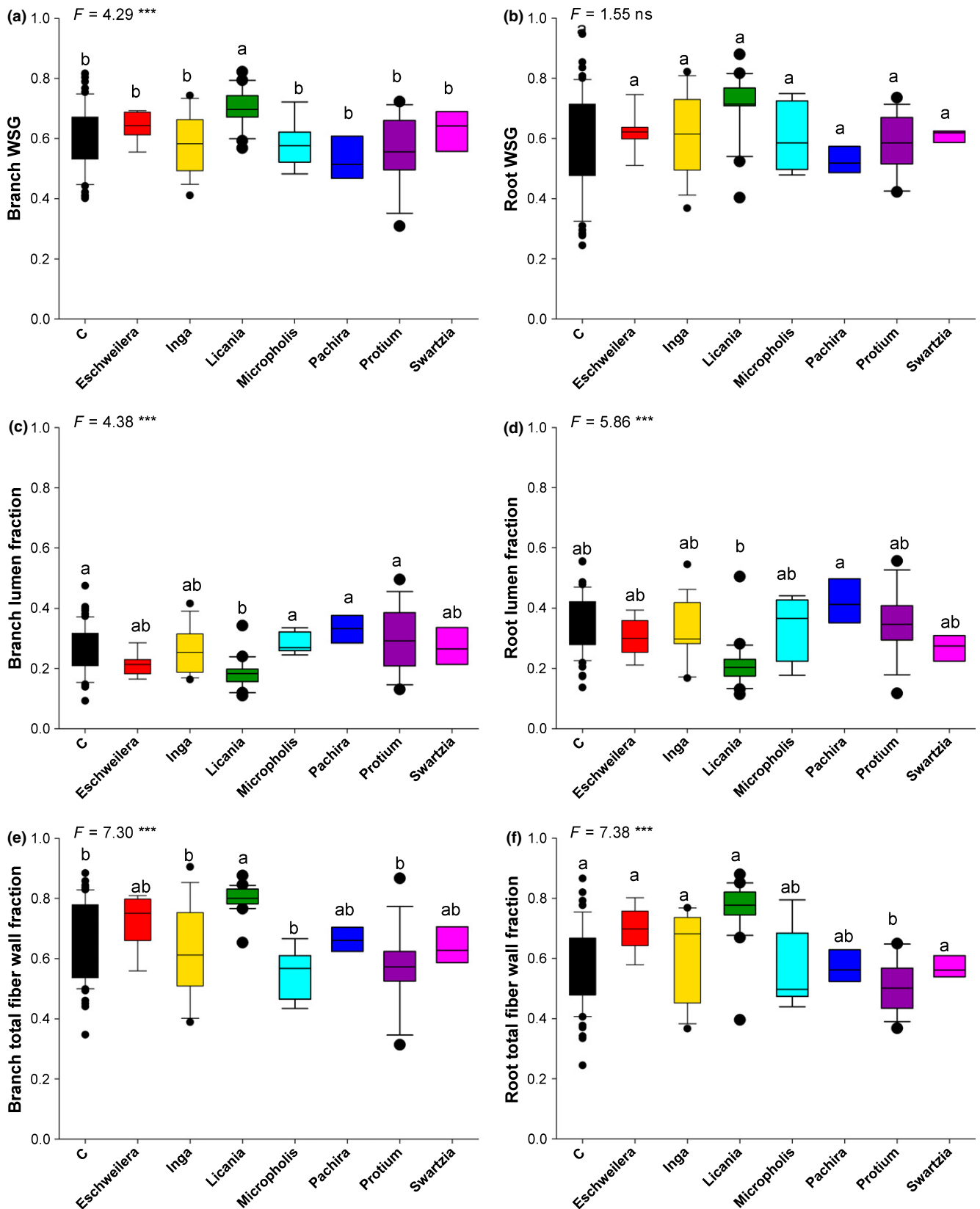


Fig. 5 Boxplots of branch and root (a, b) wood specific gravity (WSG), (c, d) lumen fraction and (e, f) total fiber wall fraction of common species and seven focal lineages. The line in the box indicates the median; the whiskers above and below the box indicate the 90th and 10th percentiles.  $F$  statistics are shown with significance test (\*,  $P < 0.05$ ; \*\*,  $P < 0.01$ ; \*\*\*,  $P < 0.001$ ; ns, nonsignificant); *post hoc* Tukey's HSD (Honestly Significant Difference) test is indicated in bold letters. Colors indicate our seven focal phylogenetic lineages (red, *Eschweilera*; yellow, *Inga*; green, *Licania*; cyan, *Micropholis*; blue, Bombacoideae (*Pachira*); purple, *Protium*; pink, *Swartzia*), while common species (C) are indicated in black. See Table 1 for trait abbreviations.



Additionally, we found that branch and root vascular traits were significantly correlated, with no differences between branch and root vessel sizes. Our results therefore seem to diverge from the paradigm predicting linear tapering of vessels from belowground to aboveground compartments (West *et al.*, 1999; McCulloh *et al.*, 2003) and instead support the pipe model theory predicting no change in wood anatomical traits between belowground and aboveground conduction systems (Shinozaki *et al.*, 1964; Tyree & Ewers, 1991; Blonder *et al.*, 2011). However, Schuldt *et al.* (2013) found evidence for humpback variation in vessel traits along small roots (2–5 mm), strong roots (> 50 mm), trunk and twigs in five tropical tree species and suggested that vessel size in aboveground and belowground organs may instead be related to segment diameter. This explanation could also apply to our results, because branch and root samples had similar diameters in our study. Yet branch wood vascular traits were more strongly correlated among themselves than with root wood vascular traits, and vice versa, further underlying potential differences in tissue allocation between branches and roots, as suggested above (Hacke & Sperry, 2001; Pratt *et al.*, 2007). Moreover, contrary to our expectation, branches and roots showed similar parenchyma fractions, suggesting similar storage capacity in both organs. Further studies will be needed to investigate whether actual storage, notably in terms of starch grains, differs between belowground and aboveground compartments.

#### Variations in wood traits between contrasting habitats

As predicted from previous findings (Preston *et al.*, 2006; Martinez-Cabrera *et al.*, 2009; Gleason *et al.*, 2012), we found that species growing in the dry and nutrient-poor soils of white sand forests exhibited denser wood in branches and roots than species in terra firme and seasonally flooded forests. Although the three studied habitats differ in soil water availability, we found little variation in branch and root anatomical traits related to sap transport between habitats. Only wood fiber, fiber wall, lumen and parenchyma fractions mirrored variations in wood specific gravity of both branches and roots across the three habitats. Hence, species in white sand forests had greater mechanical support and lower storage capacity, but they did not exhibit lower conductivity than species in terra firme and seasonally flooded forests. Although species in seasonally flooded forests exhibited lighter wood than species in terra firme, we found no variation in anatomical traits in either branches or roots between these two habitats. Our results hence underline strong environmental filtering on wood traits related to mechanical support, but not on wood traits related to sap transport between the three contrasted habitats. This suggests that tropical trees can exhibit differential investment in mechanical support and sap transport to respond to environmental conditions.

In white sand forests, the costs of herbivory to plants are greater because the low soil resource availability makes tissue replacement more difficult (Fine *et al.*, 2006), while the frequent drought stress may increase cavitation risk (Chave *et al.*, 2009). White sand forests thus filter for species with higher mechanical strength, which could be associated with higher resistance to

herbivores and lower cavitation risk. Our results differ from previous findings on Mediterranean tree and shrub species, where the authors showed variations in wood density but also in wood vessel traits with soil water availability (Preston *et al.*, 2006). Differences in aridity between tropical and Mediterranean environments could explain this discrepancy: although tropical tree species experience drought, the aridity level and duration are much lower than in Mediterranean regions and hence may not constrain sap transport so strongly.

#### Conservatism of wood traits across phylogenetic lineages

We found evidence for strong evolutionary constraints on branch and root wood anatomy, with significant differences among phylogenetic lineages for all traits, but lineages exhibited similar variation in branch and root wood specific gravity and anatomy across habitat types. Our results thus confirm previous findings on phylogenetic conservatism of wood density at broad and narrow systematic scales (Cavender-Bares *et al.*, 2004; Chave *et al.*, 2006; Swenson & Enquist, 2007) and further underline the phylogenetic conservatism of wood anatomical traits within tropical tree genera. Hence, although the anatomical design differs across lineages, evolutionary changes in wood specific gravity appear to relate to convergent evolutionary changes in wood anatomical traits.

#### Conclusion

This study demonstrates that fiber traits are major contributors to wood specific gravity, independent of vessel traits, across branches and small woody roots of tropical tree species. Moreover, we show that environmental filtering selects for tree species with high mechanical support in dry and nutrient-poor habitats. Finally, our study provides strong evidence of phylogenetic conservatism of wood structure within tropical tree genera, but phylogenetic lability at the species level. We thus underline that different tropical tree species optimize their performance across environmental gradients by investing differently in support and transport. We further point out that the study of wood specific gravity alone obscures such differential investment in support and transport to respond to environmental conditions. As the floristic and functional composition of South American forests is strongly filtered by wind disturbance (Foster *et al.*, 1999; Read *et al.*, 2011; Butler *et al.*, 2012; Lasky *et al.*, 2013) in addition to drought stress (Engelbrecht *et al.*, 2007; Malhi *et al.*, 2009; Phillips *et al.*, 2009; Saatchi *et al.*, 2013), we conclude that biophysical explanations for tree distribution across environmental gradients in the Amazon should receive more attention in future studies.

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## Supporting Information

Additional supporting information may be found in the online version of this article.

**Fig. S1** Boxplots of branch and root wood traits by habitat.

**Fig. S2** Boxplots of branch and root wood traits of common species and focal lineages.

**Table S1** Comparison of pairwise wood trait correlation matrices among six plots representing three contrasting habitats in French Guiana

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